Meteorological Conditions Inducing Long-Distance Migration of the Brown Planthopper, *Nilaparvata lugens* Stål.

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ABSTRACT

Importance of the long-distance migration of BPH and other small insect pests have ever been increasing. Long-distance movement of BPH can be divided into two main directions, the poleward movement in the spring and equator-directed movement in the autumn. Evidences of the former have been accumulated and the movements were considered to be adaptive. Evidences of the latter have been steadily accumulated but the biological meaning has not been established yet.

The whole aspect of the long-distance migration of BPH is consisted of 3 phases, the take-off, long-distance displacement and landing. Taking off usually occurs at a limited period at dawn or dusk under a calm weather. Long-distance displacement is induced by a long-lasting wind of warm and humid which is most likely to occur at the warm sector in a frontal system. Landing is often observed under windy, rainy, or even stormy weather when a frontal system is passing over irrespective of time of the day.

Equator-directed movements were observed in late summer to autumn near the frontal system. During summer, particularly in the tropics, trivial flights of BPH are often observed, for example, flight into lights or flight from a rice field to another. Relation between the trivial flight and the long-distance flight has to be analysed.

Introduction

Since Williams (1958) categorized movements of insect by flight into two: active and passive, movement of small insects carried by air, water and other artificial agents have been considered of minor interesting from the view point of the insect migration. However, even strong fliers such as locusts were shown to be carried by the seasonal winds converging to the Intertropical Convergence Zone where rainfall was expected and ultimately vegetation is likely to be more luxuriant (Rainey, 1963). Among movements of small insects, such as agricultural and veterinary pests, many cases have been accumulated in which insects are carried by seasonal winds (Johnson, 1969; Pedgley, 1982). Most cases occur at the definite time of the year and the migration seems to be implicated in the year round life history of the species. Population of the insect is established at the area where the insect lands at least during the reproductive season. The warm and humid climate heralded by the seasonal winds favour insects directly through their growth and reproduction and indirectly through the luxuriant growth of food plants.

Williams (1957) already discussed on the two important points in the insect migration; orientation and return migration. He argued that "in the temperate regions the movements are nearly always away from the equator in the spring and towards it in the autumn, and so are closely related to temperature changes". He, however, did not refer so much to the role of wind playing in the long-distance migration of insects.

In general, migratory flights in the middle latitutdes can be categorized into two, that is, arrivals of insects carried by warm poleward wind in spring and equatorward return movements in autumn (Pedgley, 1982). There have been accumulated so many examples in the former case, such as, the potato leafhopper, *Empoasca fabae,* and the six-spotted leafhopper, *Macrosteles fascifrons,* in North America (Medler, 1962), etc. Long-distance migrations of the brown planthopper (BPH), *Nilaparvata lugens,* and the white-backed planthopper (WBPH), *Sogatella furcifera,* are remarkable examples among rice insects in the temperate Asia.

Long-distance immigration of BPH and WBPH into Japanese mainland were categorized into several types (Kisimoto, 1976). All of them were related to the warm south-west wind at the warm sector of a frontal system moving north-eastwards which appears at the middle to late rainy season in the temperate East Asia, called *bai-u.*

Concerning to the equator-directed movements of insects, Asahina *et al.* (1968, 1969, 1970) and Itakura (1973) reported that many insects, including rice planthoppers, were collected at the Ocean Weather Station "Tango", ca. 500 km south of Japanese mainland. Cheng *et al.* (1979) reported that the return migration of BPH were observed on the Chinese continent. Generally, the return flight means reorientation of migrants when they return later as individuals to the former habitat, and it should carefully be distinguished from that of individuals of a later generations (Johnson, 1969). Examples shown above apparently correspond to the latter.

Importance of the migration of BPH has ever been increasing not only from a view point of the forecast of population built-up causing hopperburn but also from view points of the spreading of rice viruses transmitted by BPH and the genetical changes of BPH population in relation to the development of new biotypes which may cause break down of resistant rice varieties and to that of BPH strains resistant to various insecticides.

Distances that migrants achieve are variable, for example, short, medium and long-range (Johnson, 1969). In the present paper, long-distance migration means a displacement of BPH population between two areas under more or less different climatic conditions which induce different rice growing practices.

Poleward Migration at the Beginning of the Reproductive Season

Poleward movement of the tropical air mass since March or April in East Asia brings rainfalls in the north side and the near south side of the front. Air temperature rises and summer plants grow after passing over of the frontal system. Northward winds induced by the frontal system may be adequate carriers of small insects if insects aloft in the air are available, as the winds are mostly warm and humid. Small insects are generally vulnerable to desiccation.

The poleward migration of insects of tropical origin signifies an introduction of population source and the beginning of population increase in the areas where the insects land. When the overwintering of the insects concerned is impossible or their populations are kept at extremely low levels during winter the immigration of adults may be conspicuous and give prominent influences on the population increase in immigrated areas.

As postulated by Kisimoto (1976), the persistent year round breeding of BPH and WBPH in East Asia is only possible in the tropics. BPH and WBPH have neither diapause nor high cold tolerance. The rice plant, their only food plant, is not enough available to sustain populations during winter and spring in the subtropical and temperate regions. The first step of the poleward movement of BPH and WBPH in 1972 was considered to have occurred in early April along with the northward movement of a trough of low pressure, which induced an elevation of temperature and considerable rainfalls. Concurrently, populations of the two planthoppers were abundantly observed in the Philippines. During the period the southeasteries provailed, which suggested that the migration source of these immigrants may be located south to south-eastwards (Kisimoto *et al.,* 1976), as shown in Fig. 1.

Cheng *et al.* (1979) reported that the year round breeding of BPH was only possible in the south of 19°N line, corresponding to the southern part of Hainan Is. where rice plants grow throughout the year. The first northward migration of the planthopper occurs from middle April to early May from the year round breeding areas. Jiang *et al.* (1981) analysed meteorological conditions during the period of the first northward movement of BPH between mid April to

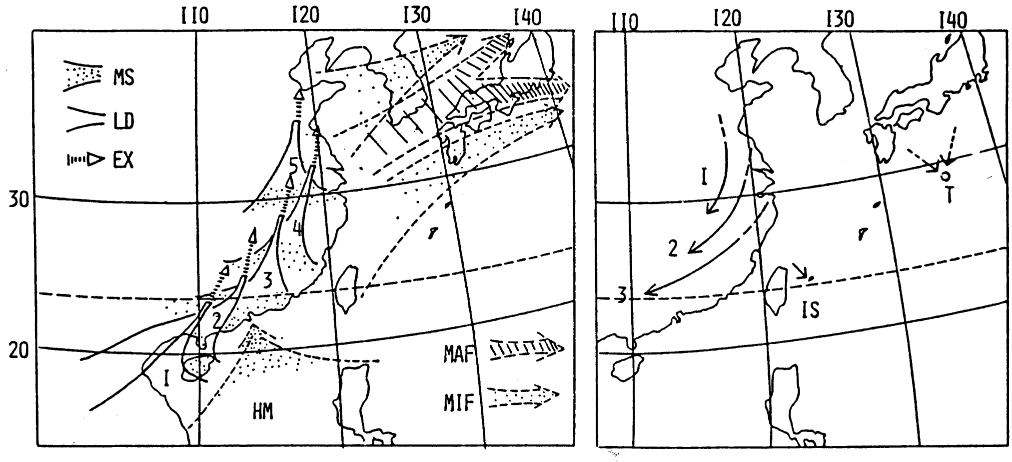

Fig. 1. Left: poleward migrations of BPH from April to August in East Asia. HM:hypotheticalmigration from the tropics into the subtropical region, MAF: route of depressions implicated in the mass immigration of BPH and WBPH into Japan mainland, MIF: those implicated in the minor immigrations (Kisimoto, 1976, Kisimoto *et al.*, 1976). Arrows with number mean the steps of migration, MS: migration source area, LD: main landing area, EX: extended landing area (Cheng *et al.*,1979).
Right: equator-directed migrations of BPH in autumn. T and arrows: southward movements of BPH and other planthoppers caught at the Ocean Weather Station (Tango) (Asahina *et al.*, 1969, 1970; Itakura, 1973), arrows with number 1-3: three steps of the return migration of BPH (Cheng *et al.*,1979), IS and an arrow: immigration of BPH into Ishigaki Is. (Tsurumachi, 1984 personal communication).

early May in 1977 and found out that SW winds prevailed. Zhu *et al.* (1982) carried out several aeroplane collections of flying planthoppers 300 to 2,000 m high above the ground over the southern part of Chinese continent and Hainan Is. April 30 to May 9 in 1978 and April 17-24 in 1979. In the two years, BPH and WBPH were captured when south-west winds blew but when south-east winds blew WBPH only were captured. They suggested that BPH might immigrate from the Indo-China peninsula. But the possibility that BPH may be carried by south to south-east winds is not deniable as BPH and WBPH tend to immigrate in a closely related manner (Kisimoto, 1976).

The following 4 steps of further northward migration of BPH were postulated by Cheng *et al.* (1979) in the east part of Chinese continent based on a comprehensive survey in 1977. The second step of migration occurred from mid May to early June; the third from mid June to early July; the fourth from early to mid July; and the fifth from late July to early August. Destined areas where the migrants are to be deposited in each step of migration moved steadily northwards up to around 35°N, as shown in Fig. 1.

In Japan mainland, immigrations of BPH and WBPH usually occur from late June to mid July, when activities of the frontal system of *bai-u* are very high (Kisimoto, 1976). Depressions implicated in the migration concerned appeared mostly in the central part of Chinese continent when the *bai-u* front is located there and moved north-eastwards along the frontal line. At the warm sector of a depression S-W wind blew for a considerable period, when immigrants were collected by various traps (Fig.1).

In Okinawa and Amami, main immigrations of BPH and WBPH occur in early June to early July when the frontal system of *bai-u* is located. The most immigrations observed in Naha, Okinawa 26°14'N 127°41'E did not occur coincidentally with those in Chikugo, Fukuoka 33° 12'N 130°30'E. A half of the immigrations observed in Naze, Amami 28°23'N 129°30'E occurred coincidentally with Chikugo and the other half with Naha (Kisimoto *et al.*, 1982). The facts strongly suggest that meteorological conditions inducing long-distance migration of BPH and WBPH do not cover such a wide area as from Fukuoka to Okinawa, the two locations being apart by 7° in the latitudinal degree from each other. On the other hand, it was already shown that when a warm and humid wind blew from south-west to north-east for a considerable period immigrations of BPH and WBPH occurred in areas stretching west-eastwards for 1,000 km or more covering the western half of Japanese mainland (Kisimoto, 1979). In United States, influxes of the potato leafhopper, *Empoasca fabae,* into the Midwest from the Gulf states were shown favored by a persistent southerly flow of maritime tropical air (Huff, 1963).

The second and the third step of the northward migration categorized by Cheng *et al.*(1979) seems to correspond to the immigrations into Okinawa and Japan mainland, respectively, but the source area of the migrants found in Japanese mainland has not been determined.

Equator-Directed Migration in Autumn

Southward migrations of the planthoppers and other small insects in the East Asia have often been observed at Tango, an ocean weather station 29°N 135°E. Asahina *et al.* (1969) collected 131 WBPH and 49 BPH on Sept. 16-25, 1967, when NW wind blew at 3-8 m/s, and 7 WBPH and 38 BPH on Oct 15-16, 1967 when NNE-ENE winds blew at 5-7 m/s. In the two cases winds were implicated in the frontal system of the autumn rainy season. Asahina *et al.* (1970) also caught many WBPH and BPH from August through Oct. 1968. Itakura (1973) caught 11 BPH, 2 WBPH, a *Laodelphax striatellus,* and 3 *Sogatella panicicola* at Tango on Sept. 7, 8 and 10, 1973, when the station was located at 100 to 400 km north of a cold front associated with the autumn rainy season. He caught a few planthoppers also at Sept. 29 and Oct. 1 and 5, and Oct. 11 and 12, 1973, at 200 to 400 km south or north of a cold or stationary front. It is interesting to note that all the weather systems when the insects were caught moved eastwards. He suggested that the migrating insects originated from western Japan.

Cheng *et al.* (1979) reported that three steps of "the return migration" of BPH were observed in East China; the first one from the end of August to mid September, the second from mid September to the beginning of October, and the third from the middle to late October. The migration sources were located in the north of 33°N at the first return migration, 31-34°N at the second, and 28-32°N at the third. The third return migration is considered to be destined to the southern part of Chinese continent. In this report, however, significance of the southward migration as the source of population increase at the destined area were not clearly discussed, while local populations of BPH at the destined area seem to be available. Tsurumachi (1984, personal communication) observed several immigration peaks of BPH and WBPH from the late August to November, 1983, in Ishigaki, Okinawa. Immigrant BPH multiplied on the second rice of the 2 croppings a year and caused damage. He supposed that the immigrants were carried by north to north-west winds as BPH on the first crop usually disappeared from Ishigaki during the fallow period before transplanting of the second crop. All the movements mentioned above were collectively shown in Fig. 1.

Trivial or Intrazonal Flight

Macropterous adults of BPH tend to take off after the teneral period of one and two days at 27.5°C and 20°C, respectively (Ohkubo, 1973, 1981). In the temperate zone, a typical daily take-off periodicity of crepuscular bimodal type was observed in the field (Ohkubo *et al.*, 1973), but in the tropics several observations (Lim, 1978; MacQullian, 1975; Ooi, 1979) showed that an evening unimodal type was common, though further observations are needed.

If planthoppers which have taken off in the evening are carried by a trivial gentle wind such as 1 to 3 m/s for a short time as usual, there will be little possibility to move such a long distance as discussed above. There must be additional meteorological factors for achievement of really long-distance migration. However, importance of these trivial flights should not be neglected in areas where staggered rice growing are practiced throughout the year. BPH migrates from paddy fields at or near the harvest to those soon after transplanting.

There have been no studies whether or not the flight behaviour of BPH at the long-distance migration differs from that of the trivial flight. There is a possibility that the long-distance migration of BPH may simply be an elongated flight induced by long-lasting wind after the take-off which may be categorized as the trivial flight when no long-lasting winds are available.

Meteorological Conditions Inducing Long-Distance Migration of Planthoppers

Meteorological conditions when BPH adults may take off much differ from those when they were caught by a tow net or attracted to the light on the sea or when they landed on a paddy field. The take-off is usually performed under a calm weather at a certain time of the day, on the contrary, landing is observed mostly under windy, cloudy, rainy, foggy or even stormy weather occurring when a frontal system is passing over. The clear difference between the two phases strongly suggests that migration source and landing area may be located far from each other in a synoptic scale. It seems, therefore, necessary to consider the whole aspect of the long-distance migration of BPH in several divided phases; the take-off, long-distance displacement, and landing.

In the temperate region, adult BPH takes off mostly within a quarter an hour at dawn or dusk, showing the crepuscular bimodal periodicity. Usually take-off at dusk is more regular than that at dawn (Ohkubo *et al.*, 1974). Light intensity at which BPH takes off most is modified by temperature as shown in Table 1. In autumn, it takes off at a higher light intensity when air temperature was low. Winds over a certain limit of speed suppress the take-off. These facts suggest that source area of the migrants appearing near the frontal system may be located considerably far from the frontal system. At the source area weather may be more or less stable and rice plants have grown up and may harbour BPH population of enough high density. Jiang *et al.* (1981) suggested that the migration source of a northward migration of BPH in June 1977 in southern Chinese continent is located far south at a distance of 3-4 longitudinal degree.

After taking off BPH, as a weak flier, is carried by winds of warm and humid. Temperature above a certain threshold is necessary for continuous wing-beating and high humidity favours long-lasting wing-beating of BPH. The temperature threshold for take-off was estimated as 18° and that for wing-beating as 16.5°C by labor-

Table 1. Biological Constants Related to Flight Behaviour of *N. lugens*

General period (Time before take-off)	female	23 hrs at	27.5°
		40	20.0
	male	21.5	27.5
		34	20.0
Take-off	(Lab)	Threshold temp. 18°C Light intensity opt. 10-40 lux with 50-80% RH, inhibited at over 100 lux or in darkness	
	(field)	Summer: crepuscular bimodal at 1-200 lux Autumn: crepuscular bimodal at 50-1000 lux at ca. 22°C Late autumn: unimodal in the evening at 50-4000 lux at ca. 18°C	
	Wind speed inhibiting take-off: 11 km/hr in the field, 5.6 m/sec. in lab.		
Wing-beating (by tethered flight)	Threshold temp. 16.5°C, lowest 10°C Continuous wing-beating time: average 10 hrs at 85% RH, max 23 hrs Exhaustion of body weight: ca. 20% loss of fresh weight.		
Height aloft in the air	300-2000 m April * 1500-2000 m Summer** 500-1000 m Autumn **		
Flight experience for settlement on food plant: more than 30 sec.			

(* Chiu, *et al.* 1982; ** Dung, 1981; others, Ohkubo, 1973, 1981; Ohkubo *et al.* 1971).

atory tests (Ohkubo, 1981). In the field the lowest temperature when immigrants of WBPH and BPH were caught by tow nets was 16.6°C when immigration occurred in May and 21.1°C and 24.6°C in two immigrations occurred in June. Immigrations of WBPH without BPH occurred at a little lower temperatures (Kisimoto, 1976). The first light trap catch in Japan tends to occur earlier in WBPH than in BPH, which suggests that WBPH has a little lower temperature threshold for take-off and/or wing-beating.

Long-lasting blowing of wind at the same direction is another important factor inducing long-distance migration. Seasonal wind is adequate from this view point. As shown in Table 2, south-west to south-south-west winds blew for several hours to 1-2 days in cases of the typical mass immigtation of BPH and WBPH into Japan mainland.

Correlation between catches on the East China Sea, 31°N 126°E and at Chikugo, the two localities being ca. 500 km apart, was generally high in WBPH but it shows irregularities in BPH (Kisimoto, 1981), that is, high correlation was shown in 1969, 1973, but it was very low in 1977, 1979. In 1980 no catches were obtained on the land while several tens of BPH were collected on the sea, as shown in Fig. 2. Wind direction, wind speed and air temperature at various levels above the sea surface surveyed at the East China Sea station by Japan Meteorological Agency in 1977 and 1978 were analysed. In 1977, as shown in Fig. 3, the northerly winds prevailed until June 26 at the sea station and no insects were caught. Then, winds veered to SSW and the air temperature rose, when insect catches began and continued until July 3rd. When wind veered to S to SE after July 4, air temperature rose further but no insects were caught. During the period no depressions moving eastwards appeared in the middle latitude of the East Asia. BPH which had been carried to the central part of the East China Sea seemed to be not carried any further. In 1978, southerly winds had prevailed until June 26 and the air temperature was already over 22° at the sea surface but no insects were caught. Then westerly winds began to blow and temperature rose further from June 29 when good catches of insects began and continued until July 7, when the survey ended. During the early part of the period when fairly strong SSW wind blew good catches were also obtained on the land, but during the later part winds veered to NW in upper air over 900 mb and wind speed decreased at all the levels, and few insects were caught on the land.

Table 2. Meteorological Factors in Each Flight Type of BPH (Kisimoto, 1976)

Flight type	Number of examples	SSW-SW winds[1] Duration (h)	SSW-SW winds[1] Max. speed (km/h)	Lowest[2] Temperature (°C)
Typical mass flight (TYP)	12	9-46 (19.3)	18-40 (32.9)	22.0-25.4
Typhoon suspended	2	8-39 (23.8)	14-35 (24.5)	23.3-24.5
Long-lasting	4	81-105 (90.5)	27-32 (29.3)	24.0-26.0
Minor flight 1	11	7-23 (15.5)	12-33 (19.2)	15.8-24.6
Minor flight 2	5	5-60 (29.6)	20-38 (27.0)	19.7-28.8
Minor flight 3	3	4-19 (13.0)	10-20 (13.0)	19.4-21.5
Stational front	3	50 (50.0)	10-33 (21.5)	22.0-24.9

1 Range and average; maximum wind speed was shown by the highest windrun per hour in a 3 h running average for each flight.
2 Lowest temperatures occurred during migrations in SSW-SW winds.

Typhoon suspended: typical mass immigration type except that a typhoon was located in the south; Long-lasting: SW winds blow for a long time at the edge of an anticyclon.

Rosenberg *et al.* (1983) suggested that the migration source of BPH caught on the central part of the East China Sea, 31°N 127°E in 1973 and 31°N 126°E in 1981 were located in the coastal area of the Chinese continent between 23° to 30° and the northern half of Taiwan and Ryukyu Islands using wind trajectory analyses.

Landing of the insects aloft in the air seems to be affected by various factors. A certain

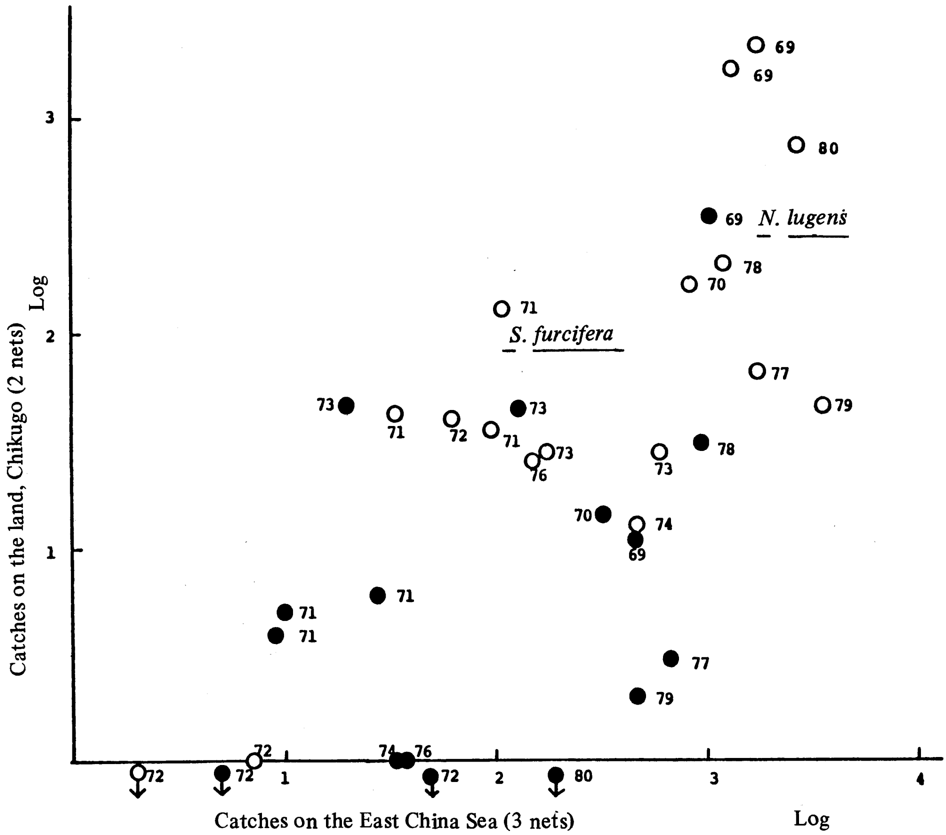

Fig. 2. Correlation between simultaneous planthopper catches (male and female) on the East China Sea and on-the land (Chikugo, Fukuoka), 1969-1980.

meteorological factors, such as, down air stream of low temperature may force the insects to land. The others are biological factors, such as, energy exhaustion and behavioural response.

Sudden mass appearances of BPH and WBPH near the cold front of a frontal system irrespective to time of the day strongly suggest that the meteorological factors seem to be primary important (Kisimoto, 1971, 1976).

Time that a planthopper persists being aloft in the air may be physiologically controlled by the total amount of flight fuel that the insect carries. The average and maximum period of the continuous wing-beating of BPH in laboratory were estimated as 10 and 23 hrs, respectively (Ohkubo, 1981), but the values seem to be rather low to explain the immigrations of BPH observed under natural conditions. Field populations of BPH tended to have higher wing-beating capabilities than those of laboratory colonies (Baker *et al.,* 1980). As discussed by Kisimoto (1976) a typical mass immigration of BPH and WBPH were considered to have occurred at areas of over 2,000 km wide in two days. There is a possibility that migrants may rest on the sea surface and retake off (Asahina & Tsuruoka, 1968), but it is least likely that the migrants can refuel. On the land, immigrants are often attracted to light trap or yellow pan water trap soon after landing, but no proofs have been available whether they might perform further long-distance displacement or not. An exponential decrease of immigrant density of BPH and WBPH along with the distance leeward from the west end of Japanese mainland (Kisimoto, 1979) suggests that the number of insects which land at a certain locality is correlated to the density of insect aloft in the air and least likely correlate

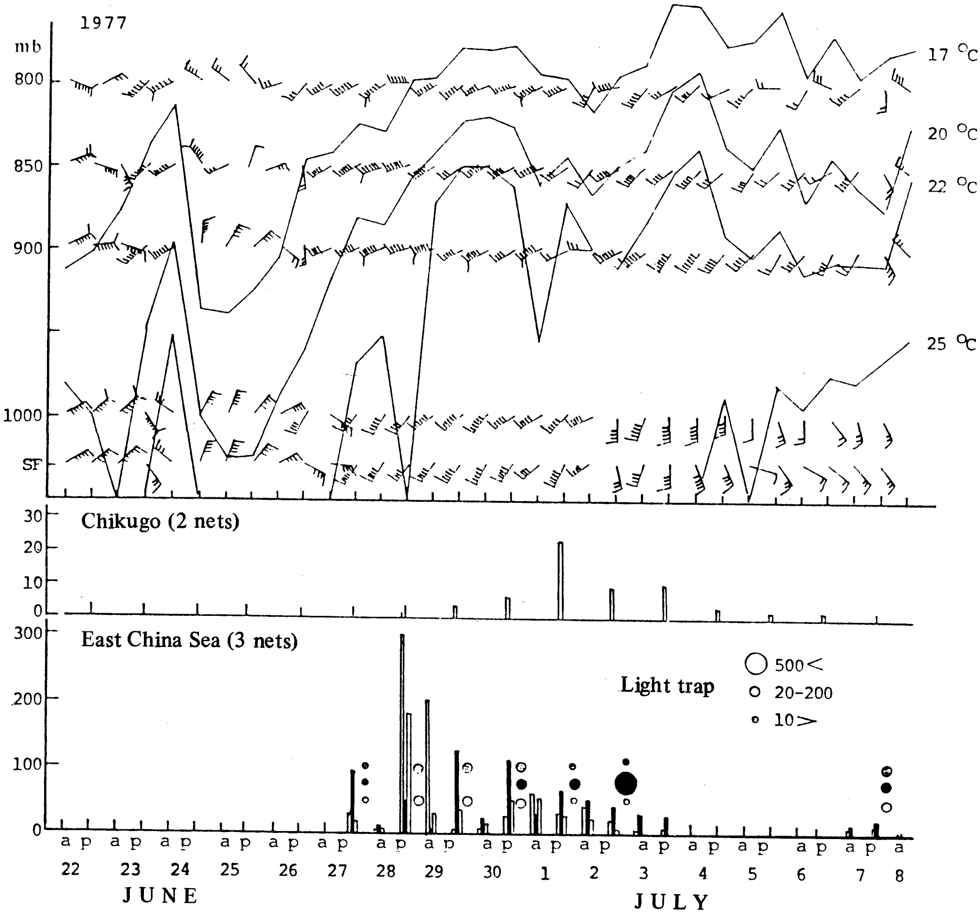

Fig. 3. Migration surveys in 1977. Upper: wind direction, wind speed and air temperature at various levels above the sea surface (SF) on the East China Sea, 31 °N 126°E.
Middle: numbers of planthoppers caught by 2 tow nets at Chikugo, Fukuoka.
Lower: numbers of planthoppers caught by 3 tow nets (bars) and those attracted by lights on the board and caught by aspirator (circles).
a: 9 o'clock and p: 21 o'clock, tow nets were emptied every 3 hours and the catches at the preceding half day were totaled. Open bars and circles: *Sogatella furcifera*, closed ones: *Nilaparvata lugens*, stippled ones: *Laodelphax striatellus*.

to biological factors controlling the flight behaviour of the insect.

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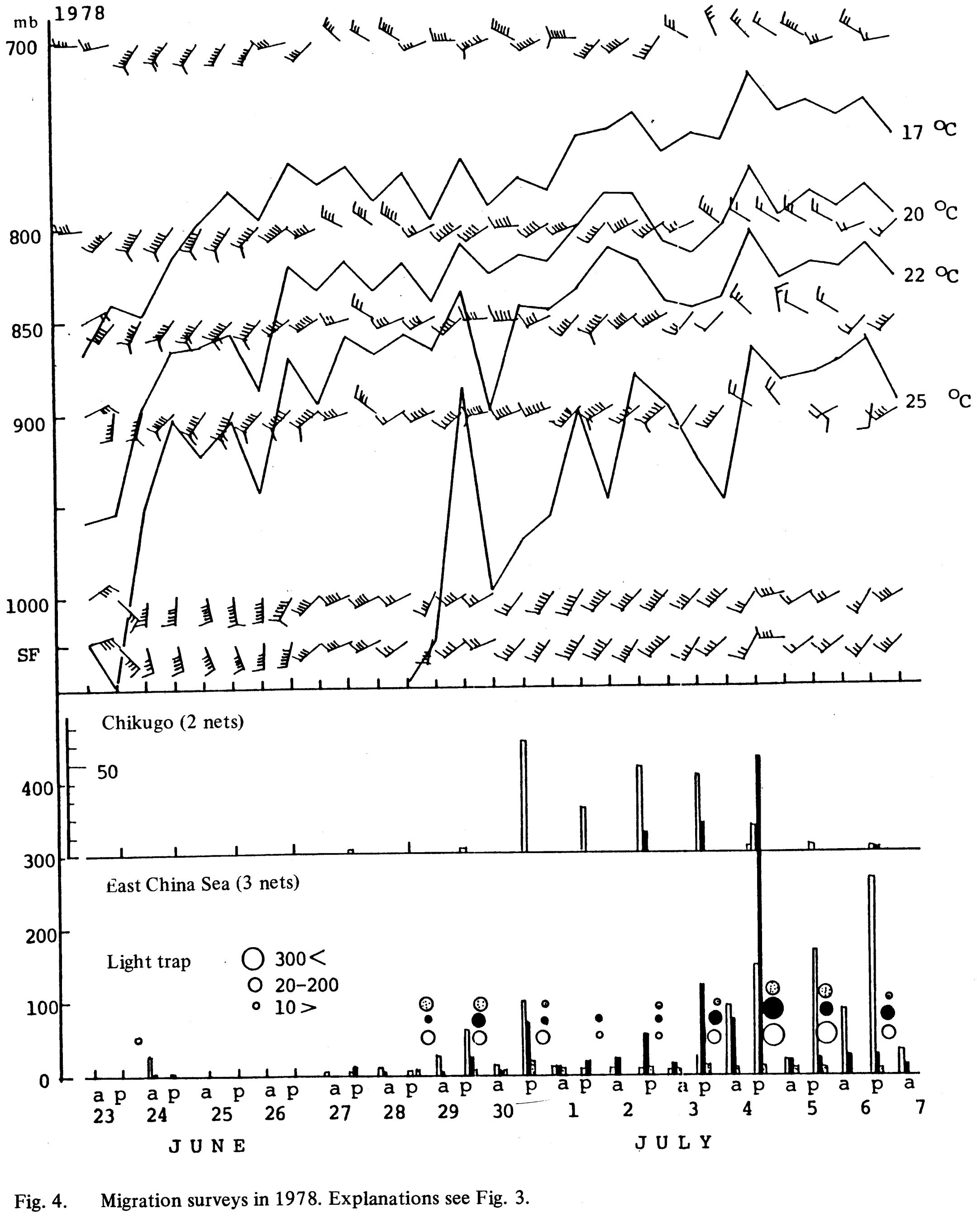

Fig. 4. Migration surveys in 1978. Explanations see Fig. 3.

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